# Serial position curves in spatial memory of rats

Bolhuis, J J; van Kampen, H.S.

*Published in:*
Quarterly journal of experimental psychology section b-Comparative and physiological psychology

*DOI:*
10.1080/14640748808402314



*Publication date:*
1988

THE QUARTERLY JOURNAL OF EXPERIMENTAL PSYCHOLOGY, 1988 *40B* (2) 135–149

# Serial Position Curves in Spatial Memory of Rats: Primacy and Recency Effects

Johan J. Bolhuis and Hendrik S. van Kampen

*University of Groningen, Haren, The Netherlands*

Memory for lists of items was tested in rats ($N = 18$) in an 8-arm radial maze. In Experiment 1 trials consisted of a study phase, in which the rat could freely choose five arms to obtain a food reward, and a test phase in which the animal was presented with a choice between a novel and a previously visited arm. The rat received additional food reinforcement only when visiting the novel arm. The two phases of a trial were separated by a retention interval of 30 sec or of 4, 16 or 60 min. It was found that recall of the five free arm choices was related to the serial position of the previously visited arm. There was a significant recency effect at the 30-sec delay. With longer retention intervals this disappeared, and a significant primacy effect could be observed. In Experiment 2 the same animals were given forced arm entries during the study phase and delays of 30 sec or 4 or 16 min before the test phase. Again, there was a trend towards a recency effect after the shorter delays and a significant primacy effect after the 16-min interval. These results show that, in the recall of lists of spatial items, rats have serial position curves with primacy and recency effects, depending on the length of the retention interval.

The serial position curve is a well-known phenomenon in human memory research that has had an important influence on the development of theories of memory (Murdock, 1962; Atkinson & Shiffrin, 1968; Craik, 1970; Rundus, 1971; Baddeley, 1976). It occurs when, for example, subjects' memory for a list of verbal items is tested in a free recall task. A typical finding is that recall of items at the beginning and at the end of the list is better than that of items in the middle part. This is known as the primacy and the recency effect, respectively.

Requests for reprints should be sent to J. J. Bolhuis, University of Groningen, Zoological Laboratory, P.O. Box 14, 9750 AA Haren, The Netherlands.

We are grateful to Jan Bureš, Jerry Hogan, Jaap Kruijt and Arjen Strijkstra for their valuable comments, and to Piet Klont, Michel Hoes and Thea van der Schee for their help.

For a long time studies of memory for lists of items in animals yielded only recency effects, which led to the hypothesis that the primacy effect is a result of processes typical of human verbal learning (e.g. MacPhail, 1982). For instance, Gaffan (1977) and Gaffan and Weiskrantz (1980) found recency effects, but no primacy effects, in matching to sample and non-matching to sample recognition tasks in rhesus monkeys. MacPhail (1980) reported flat serial position curves in memory for lists of items in a recognition task in pigeons. Thompson and Herman (1977), testing a dolphin's memory for lists of sounds, found a serial position curve with a recency effect, but no evidence for a primacy effect. Unlike free recall procedures, in probe recognition tasks with human subjects often only recency effects or flat serial position curves are found (see Gaffan, 1983). However, Sands and Wright (1980) and Roberts and Kraemer (1981) reported serial position curves with a clear primacy effect in a visual recognition task in monkeys as well as humans. The authors suggested that primacy effects might be typical of primate memory in general.

Olton and Samuelson (1976) introduced the radial arm maze as a means of studying spatial memory in the rat. These authors reported that errors made in a trial were mainly repetitions of the first few arm choices, indicating a recency, but not a primacy effect. Roberts and Smythe (1979) studied rats' memory for lists of items in a number of spatial tasks, including the radial maze. Using different list lengths they repeatedly found clear recency effects, but no indication of a primacy effect. DiMattia and Kesner (1984) tested memory of rats in an 8-arm radial maze, using a procedure similar to that of Roberts and Smythe (1979). Rats were given five forced entries of arms, after which they were allowed to choose freely between a previously visited arm and an arm that had not been visited before in that particular trial. For one group of rats the additional reinforcement could be obtained in the novel arm, whereas the animals in another group received a reward upon revisiting the previously chosen arm—a 'win–shift' and a 'win–stay' procedure, respectively (cf. Olton, Becker, & Handelmann, 1979; Olton & Schlosberg, 1978). DiMattia and Kesner found clear recency effects but no primacy effects in the animals trained with the win–shift procedure, similar to what Roberts and Smythe (1979) had reported. In contrast, the animals in the win–stay task showed a serial position curve with primacy as well as recency effects, albeit only after the animals had received a large number of trials. The authors concluded that the occurrence of primacy effects is dependent on "effortful information processing", such as was supposed to be engaged in the difficult win–stay task (cf. Olton & Schlosberg, 1978). Kesner and Novak (1982) and Kesner, Measom, Forsman and Holbrook (1984) introduced a procedure to test rats' memory for order information in a radial maze. Primacy and recency effects could be observed with this procedure. The animals needed a large number of trials to reach performance that exceeded chance levels.

Kesner et al. (1984) attributed the occurrence of a primacy effect to the extreme difficulty of this task, for which "effortful information processing" is required.

Recently, Wright, Santiago, Sands, Kendrick, and Cook (1985) tested memory for lists in a probe recognition task with visual stimuli in humans, monkeys, and pigeons. These authors found primacy and recency effects in all three species, depending on the length of the retention interval. At short intervals, a recency effect was found, whereas a primacy effect became apparent at longer delays. With intermediate retention intervals, both primacy and recency effects could be observed simultaneously.

In the study of DiMattia and Kesner (1984), as well as in that of Roberts and Smythe (1979), which also used rats in a radial maze, retention was tested almost immediately after the study phase of a trial. This raises the possibility that, analogous to the findings of Wright et al. (1985), primacy effects might be found in rats in a radial maze task when longer retention intervals are used. Also, in the former two studies a forced-entry procedure was used—that is, the animals could not freely choose arms in the study phase of the experiment. Unpublished results of experiments in our laboratory suggest that the use of a forced entry procedure may result in rapid forgetting of information concerning visited arms, which could affect the shape of the serial position curve.

In the present experiments, memory for lists of visited arms in a radial maze was re-investigated, using both a free-choice and a forced-entry procedure and introducing retention intervals of varying length.

## EXPERIMENT I

In this experiment, a procedure similar to that of Roberts and Smythe (1979) was used, except that rats were given five free choices of arms during the study phase of each trial. Furthermore, various delays were introduced between the study phase and the test phase.

### Method

*Subjects.* Twenty-one male albino rats (Wistar) were used. The animals were six months old at the beginning of the experiment. They were housed in three cages in a room with constant temperature, and a L/D:12/12 schedule (lights on from 0800 to 2000). One week before the start of the experiments the rats were put on a 23-h food deprivation schedule. During the experiment they had access to food (Hope Farms) after each trial for as long as needed to keep the animals at 85–90% of their free-feeding bodyweight. Water was available ad libitum throughout the experiment.

*Apparatus.* The radial maze had been used in previous experiments (Bolhuis, Bijlsma, & Ansmink, 1986; Strijkstra & Bolhuis, 1987) and was similar to that described by Olton and Samuelson (1976). The central platform was 34 cm in diameter. The eight arms were 86 cm long and 7 cm wide with 3-cm-high side walls; 5 cm from the end of each arm was a recessed food cup 1 cm deep and 2 cm in diameter. The maze was placed 50 cm above floor level in a room with abundant visual cues. Around the edge of the central platform a 16-cm-high wall of wooden segments was made, with an opening at the beginning of each arm, in which transparent Perspex guillotine doors could be placed. The maze was made of wood and painted matt grey.

*Procedure.* At the beginning of the experiment trials were run without the guillotine doors in the maze. On the first day the rats were allowed to adapt to the apparatus in three sessions of 10 min, during which they were placed on the maze in groups of 3 or 4 and allowed to eat raisins that had been put into the foodcups and scattered through the maze. The next day this procedure was repeated, but this time the rats were placed into the apparatus individually. Training was started when the rats had learned to retrieve the raisins from the food cups. At the start of a trial a small raisin was placed into the food cup of each arm. A rat was placed on the central platform and allowed to retrieve all of the raisins. The animals received two trials each day, five days a week, with at least 2.5 h between the two trials. The rat was considered to make an error when it entered with all four paws an arm that had already been visited in that particular trial—that is, in an errorless trial the animal would visit eight different arms in the first eight choices. For actual testing, only those rats were used that visited all 8 arms within 10 min. Two animals did not reach this criterion during training and were excluded from the experiment. One rat became ill and was also excluded.

After 8 trials, the mean number of errors had reached a level of 0.5 ($\pm$0.15, SEM). The maze was now equipped with guillotine doors that could be operated by means of overhead lines. At the start of a trial the rat was placed on the central platform, with all doors lowered. After 5 sec all doors were raised simultaneously. When the animal entered an arm, the doors of all the other arms were lowered. Once the rat had returned to the central platform, the door of the visited arm was also lowered; after 5 sec all doors were raised again simultaneously. After the last choice the animal was allowed to return to the central platform and was removed from the apparatus. The use of guillotine doors in this way has been shown to eliminate response chaining of the animals (Olton & Werz, 1978; Bolhuis et al., 1986). Training continued until asymptotic performance had been reached (0.33 errors after 14 trials).

During the remainder of the experiment, trials consisted of a study phase

and a test phase, separated by a retention interval ranging from 30 sec to 60 min. In the study phase of a trial the animal could choose five arms freely and retrieve the raisins. The guillotine doors were opened and closed as in the preceding phase of the experiment. The rats took approximately 1.5–2 min to complete the study phase. After the fifth choice the rat was allowed to return to the central platform, after which it was removed from the maze and placed into its home cage. In all experiments, during longer intervals trials were run with one or more of the other rats. After the retention interval the rat was again placed on the central platform and allowed to choose once between two arms, the doors of which were opened simultaneously. One of the two arms had been visited earlier in that particular trial, the other had not. Only the arm that had not been visited before contained an additional reward. The unvisited arm for the test phase was chosen such that it was as close as possible to the already visited arm. The position of the unvisited arm (to the left or the right of the visited arm) was randomized across trials. The visited arm used in the test phase could be any of the arms in the sequence of five visited during the study phase. The serial position of the visited arm (1, 2, 3, 4, or 5 in the first series of trials of Part 1 and 1, 3, or 5 in the rest of the experiment), that served as one of the alternatives in the test phase, was randomized across trials. Each serial position was tested the same number of times for one retention interval during each part of the experiment. During an experimental trial only one test of a serial position was given to each animal.

In *Part 1*, 25 consecutive trials were run with a retention interval of 30 sec, with 5 trials for each serial position. This procedure was repeated with a retention interval of 60 min. The animals received an additional 15 trials with a 60-min delay, in which only positions 1, 3, or 5 were tested in the test phase.

In *Part 2*, retention of Choices 1, 3, and 5 was tested using delays of 30 sec, 4 min, and 16 min (2 trials per position, per delay) and of 60 min (4 trials per position), in ascending order.

In *Part 3* the radial maze was transferred to another experimental room, with different environmental cues. Immediately after the transfer, retention of Choices 1, 3, and 5 was tested, using delays of 30 sec, 4 min, and 16 min, respectively (2 trials per position, per delay).

In *Part 4* the animals were tested in the same room as in Part 3. Again, delays of 30 sec, 4 min, and 16 min were used (2 trials per position, per delay), but this time the different delays were introduced in a quasi-random order (cf. Strijkstra & Bolhuis, 1987).

*Statistical analysis.* For each part of the experiment the effects of delay and serial position on the rats' performance (percentage correct choices) were analysed by means of a two-factor analysis of variance (ANOVA) with repeated measures on both factors. When there was a significant interaction

between the two factors, the effects of serial position at each delay were analysed by means of a one-factor analysis of variance with repeated measures (Winer, 1971). Differences between pairs of means were tested with Newman-Keuls tests (Winer, 1971).

## Results and Discussion

*Part 1.* Figure 1 shows the mean percentage of correct choices for the 25 trials with a delay of 30 sec and the subsequent 25 trials with a delay of 60 min, during which retention of all five positions was tested. A two-factor ANOVA revealed a significant effect of delay, $F(1, 17) = 19.01$, $p < 0.01$, but not of serial position [$F(4, 68) = 1.23$, $p > 0.10$]. As the interaction between these two factors was nearly significant, $F(4, 68) = 2.38$, $p = 0.06$, separate one-factor ANOVAs were performed on the results at the two delays. There was a significant effect of position at the 30-sec delay, $F(4, 68) = 3.81$, $p < 0.01$. Newman-Keuls tests revealed a significant difference between the mean at Position 5 and all other means, $p < 0.05$, indicating a significant recency effect. There was no significant effect of position at the 60-min delay [$F(4, 68) = 0.98$, $p > 0.10$].

The results of the subsequent 15 trials with a 60-min delay, in which only Positions 1, 3, and 5 were tested, were combined with the results of the tests of these three positions of the previous 25 trials with a 60-min delay. These combined results are shown in Figure 2 (top), together with those of Positions 1, 3, and 5 of the trials with a 30-sec delay that had been run earlier.

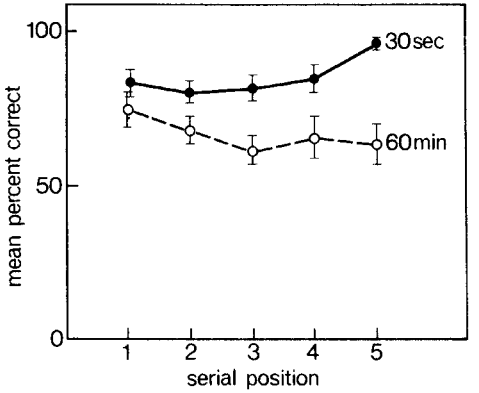


FIG. 1. Mean percentage correct choices (± SEM) in the test phase of the first part of Experiment 1, after retention intervals of 30 sec and 60 min, in relation to the serial position of free choices of arms during the study phase ($N = 18$). In this part of the experiment, recall was tested for all five serial positions.

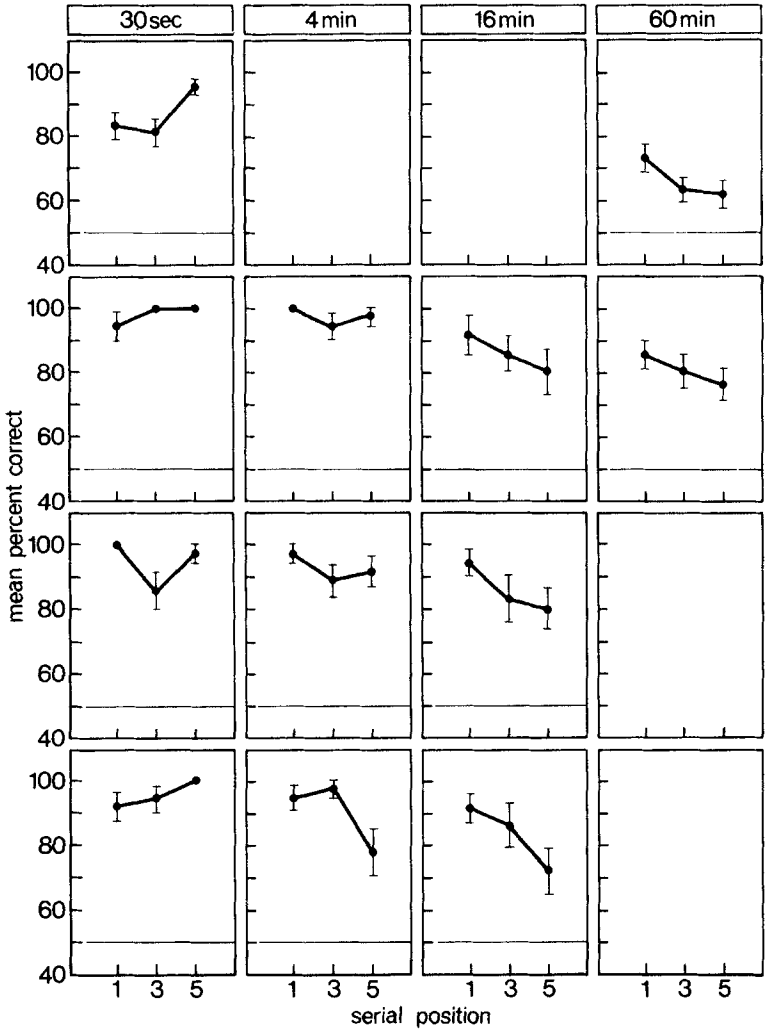


FIG. 2. Mean percentage correct choices (± SEM) in the test phase of Experiment 1, Parts 1–4, in relation to the serial position of free choices of arms during the study phase. The four rows show the results of the four parts of the experiment, respectively ($N = 18$).

A two-factor ANOVA performed on these values revealed a significant effect of delay, $F(1, 17) = 29.50$, $p < 0.001$, but not of position [$F(2, 34) = 2.24$, $p > 0.10$]. There was a significant interaction between these two factors, $F(2, 24) = 9.10$, $p < 0.001$—that is, the effect of serial position on the mean percentage of correct choices depends on the length of the retention interval.

The means between the two delays were significantly different at Positions 3 and 5, $p < 0.05$, but not at Position 1. A one-factor ANOVA for all trials at the 60-min delay revealed a significant effect of position, $F(2, 34) = 3.71$, $p < 0.05$. The mean at Position 1 differed significantly from the other two means, $p < 0.05$, indicating a significant primacy effect. As seen above, the data for the 30-sec delay showed a significant recency effect.

*Part 2.* The results of Part 2 are also illustrated in Figure 2. Performance after the 30-sec delay was better than it had been after the 30-sec delay in Part 1. A two-factor ANOVA on the results of this delay in Parts 1 and 2 revealed significant effects of training, $F(1, 17) = 31.18$, $p < 0.001$, and of serial position, $F(2, 34) = 8.38$, $p < 0.005$, but no significant interaction between these two factors [$F(2, 34) = 2.56$, $p = 0.09$]. A two-factor ANOVA performed on the results of the 60-min-delay trials of Part 1 and Part 2 also revealed significant effects of training, $F(1, 17) = 13.16$, $p < 0.005$, and of position, $F(2, 34) = 3.99$, $p < 0.05$, but no significant interaction between these two factors [$F(2, 34) = 0.28$, $p > 0.10$]. These effects of training on performance are concordant with the findings of Roberts and Smythe (1979) and Strijkstra and Bolhuis (1987). A two-factor ANOVA on the results of Part 2 revealed a significant effect of delay, $F(3, 51) = 9.61$, $p < 0.001$, but no significant effect of position [$F(2, 34) = 1.63$, $p > 0.10$] nor a significant interaction between these two factors [$F(6, 102) = 1.17$, $p > 0.10$].

*Part 3.* Because prolonged training might have affected performance in subsequent trials in Part 3, only the results of the 30-sec delay were compared to those of Part 2, to investigate whether transfer to the other room affected rats' performance. A two-factor ANOVA revealed no significant effect of serial position [$F(2, 34) = 1.69$, $p > 0.10$] nor of transfer [$F(1, 17) = 2.13$, $p > 0.10$]. The latter finding is somewhat surprising in view of findings by Suzuki, Augerinos, and Black (1980), showing substantial effects of changing extra-maze cues on performance in the radial maze. A significant interaction between these two factors was found, $F(2, 34) = 5.01$, $p < 0.025$, indicating that the effect of transfer to the testing room on performance was dependent on the serial position. A two-factor ANOVA on the results of Part 3 revealed a significant effect of delay, $F(2, 34) = 5.15$, $p < 0.025$, and of position, $F(2, 34) = 3.81$, $p < 0.05$, but no significant interaction between these two factors [$F(4, 68) = 0.79$, $p > 0.10$].

*Part 4.* The bottom row of Figure 2 shows the results of Part 4. A two-factor ANOVA revealed significant effects of delay, $F(2, 34) = 4.45$, $p < 0.025$, and of serial position, $F(2, 34) = 9.04$, $p < 0.001$, and a significant interaction between these two factors, $F(4, 68) = 2.99$, $p < 0.025$. One-factor ANOVAs performed on the results of the different delays only revealed a significant

effect of position at the 4-min delay, $F(2, 34) = 8.81$, $p < 0.001$. The mean at Position 5 differed significantly from the other two means, $p < 0.05$, indicating a negative recency effect (Craik, 1970; Mazuryk,1974).

A two-factor analysis of variance performed on the results of the 30-sec, 4-min, and 16-min delays of Parts 2 to 4 combined revealed a significant interaction between the delay and serial position factors, $F(4, 68) = 2.79$, $p < 0.05$. Subsequent one-factor ANOVAs performed on the combined results of Parts 2, 3, and 4 of the three different delays revealed significant effects of position at the 4-min and the 16-min delay, $F(2, 34) = 3.69$, $p < 0.05$, and $F(2, 34) = 3.54$, $p < 0.05$, respectively, but not at the 30-sec delay [$F(2, 34) = 1.61$, $p > 0.10$]. Newman-Keuls tests revealed that the means at Position 1 of the 4-min and the 16-min delay differed significantly from the other two means, $p < 0.05$, indicating a primacy effect at both delays.

It is conceivable that the significant primacy effects found in this experiment were a result of response chaining or preferences in the animals for a particular arm to be visited first in a trial. Analysis of the patterns of choice of individual rats did not reveal response chaining. First arm entries for each animal were analysed for the 40 60-min-delay trials of Part 1, where a significant primacy effect had been found. Chi-square tests showed that 5 of the 18 rats had a distribution of first arm choices that differed significantly from random choice ($p < 0.05$). In order to evaluate the contribution of these animals to the primacy effect, a "primacy score" was calculated for each rat. This was the percentage of correct choices at Position 1 minus the percentage of correct choices at Position 5. Linear regression analysis performed on these scores and the corresponding $\chi^2$ values for each rat did not show a significant correlation between these two variables ($r = -0.0054$, $p = 0.983$).

It could be argued that an "odour trail" of an individual rat would be more salient after a short than after a long retention interval as trials were run with other animals during the latter. Although such differences might have affected the results, this is unlikely on the basis of previous studies, in which it was shown that intramaze cues, such as "odour trails", do not play a significant role in the animal's performance (e.g. Bolhuis et al., 1986).

## EXPERIMENT 2

Analysis of the patterns of choice and arm preferences for the first choice in the study phase in Experiment 1 already indicated that it is unlikely that the primacy effect after the longer delays was a result of response biases. Experiment 2 was performed in order to rule out such explanations for the primacy effect by explicitly preventing response biases in the animals. This was achieved by subjecting rats to a forced entry procedure during the study phase (cf. Roberts & Smythe, 1979; DiMattia & Kesner, 1984).

## Method

*Subjects.* The same rats ($N = 18$) were used as in Experiment 1. After the animals had not been tested and had received water and food (Hope Farms) ad libitum for a period of 6 weeks, they were transferred back to the original testing room. They were maintained under the same conditions as before. One week before the start of Experiment 2, the rats were put on a 23.5-h food deprivation schedule.

*Apparatus.* The same radial maze was used as in Experiment 1.

*Procedure.* The rats received a number of trials in which they could freely enter all arms of the maze and retrieve the raisins. After eight such trials the mean number of errors in the first 8 choices was 0.39 ($\pm 0.12$, SEM). The procedure for the remainder of the experiment was similar to that of Experiment 1, except that the animals were given five forced arm entries in the study phase of the experiment—that is, only one guillotine door was opened at the beginning of the trial. After the rat had returned to the central platform, again one door was opened. This was repeated five times. The order of the different arms entered was randomized. After the study phase, the rat was placed into its home cage. Following a delay of 30 sec, 4 min, or 16 min, the rat was put back on the central platform, where it was given a choice between an already visited arm (Choice 1, 3, or 5) and a novel arm, as in Experiment 1. Both the different delays and the position of the arm that was used in the test phase were given in a random sequence. For each of the different delays, each serial position was tested three times.

## Results and Discussion

The mean percentage of correct choices in the test phase for the three serial positions and the three delays is shown in Figure 3. A two-factor analysis of variance with repeated measures on both factors (delay and serial position) revealed a significant interaction between the two factors, $F(4, 68) = 3.96$, $p < 0.01$—that is, the effect of serial position on performance is dependent on the length of the retention interval. Separate one-factor repeated measures ANOVAs for the different delays revealed a significant effect of position on the percentage of correct choices at the 16-min delay, $F(2, 34) = 3.81$, $p < 0.05$, but not at the other two delays [$F(2, 34) = 2.66$, $p = 0.08$ for 30 sec and $F(2, 34) = 1.38$, $p > 0.25$ for 4 min]. Newman-Keuls tests for the results of the 16-min delay showed a significant difference between the mean at Position 1 and both of the other means ($p < 0.05$). Thus, at the 30-sec delay there was a trend towards a recency effect, whereas there was a significant primacy effect after the 16-min delay.

These results confirm those of Experiment 1 and render it unlikely that the

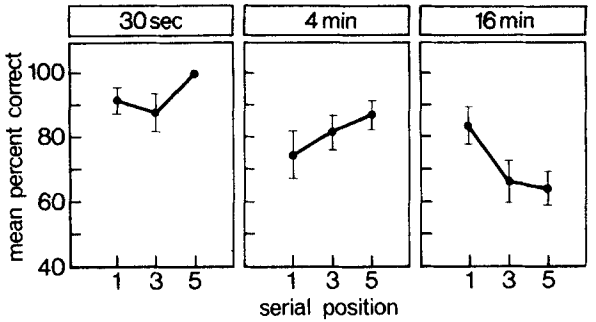


FIG. 3. Mean percentage correct choices (± SEM) in the test phase of Experiment 2 after three different retention intervals, in relation to the serial position of forced arm entries during the study phase ($N = 18$).

primacy effects in that experiment were a result of the free choice procedure that was employed.

## GENERAL DISCUSSION

The results of the present experiments suggest that both primacy and recency effects occur in the serial position curves of rats in a radial arm maze. In Experiment 1, using a free choice procedure, significant primacy and recency effects were found, depending on the length of the retention interval. Analysis of the patterns of choice in Experiment 1 and the results of Experiment 2, where a forced entry procedure was used, showed that the primacy effects were not a result of arm preferences occurring in the free choice procedure.

In previous experiments in which serial-position-related recall of spatial item information was tested in rats (Roberts & Smythe, 1979; DiMattia & Kesner, 1984), only recency effects were found, except when the animals received extensive training with a "win–stay" procedure (DiMattia & Kesner, 1984). In both these previous studies, retention intervals of only a few seconds were used. The present results show that after longer delays significant primacy effects may occur, whereas the recency effect disappears. These delay-dependent serial position effects are somewhat similar to those that Wright et al. (1985) reported for probe recognition tasks in humans, monkeys, and pigeons. There are several differences between the latter results and those of the present study. First, the time course for the occurrence of both primacy and recency effects is different in the two studies. Wright et al. (1985) found that the change from recency to primacy effects occurred in approximately 10 sec in pigeons, 30 sec in monkeys, and 100 sec in humans. The results of the present study suggest that a change in the serial position curve from recency to primacy takes place in several minutes. This is

consistent with the general finding that spatial working memory is much more robust than other forms of working memory (e.g. MacPhail, 1986; Olton, 1985). Second, recall of the first position of the list in the present study is relatively stable, whereas in the experiments by Wright et al. (1985) recall of the first item in the list improved with increasing retention interval in all three species. The authors attribute this effect to dissipation of retroactive interference with increasing retention interval. A possible explanation for the absence of such an effect in the present study is a "ceiling effect"—that is, although at the 30-sec delay recall of the first item of the list is worse than that of the last item, it is already close to the theoretical maximum of 100%. It is of course possible that the primacy effects in the present experiments reflect a different mechanism than those in the studies of Wright et al. (1985) and others. For instance, a difference between the present experimental design and that of Wright et al. (1985) and Gaffan and Weiskrantz (1980) is that in the latter studies several lists were presented during an experimental session, whereas in the present experiments only one list was tested in a session.

Gaffan (1983) has provided a critique of two studies in which primacy effects were found in visual recognition memory in monkeys. The author points out that both in the study of Roberts and Kraemer (1981) and in that of Sands and Wright (1980), list presentation was initiated by a response (pressing a key or holding down a lever) of the animal. Gaffan suggests that with this procedure, primary items in the list have attentional advantages over subsequent items, resulting in better memory for the former. This contention is supported by results of experiments by Gaffan (1977) and Gaffan and Weiskrantz (1980), in which each item in the list was treated equally and where no primacy effects were found. Gaffan's criticisms could also be applied to the study of Wright et al. (1985) where a procedure similar to that of Sands and Wright (1980) was used. However, when such an explanation is adopted, it is not clear why primacy effects should only become apparent after a retention interval of a certain length.

In the present experiment initiation of the list was not dependent upon a response by the rat. It could be argued that placing the animal into the maze shortly before the start of a trial creates some kind of attentional advantage for the first item. Lieberman, McIntosh, and Thomas (1979) have reported findings that are relevant to this issue. The authors found that rats could learn a spatial discrimination task in a T-maze in which food reward was delayed for 1 min, provided the animals were handled (or exposed to intense light or noise) shortly after the choice had been made. Lieberman et al. suggested that handling facilitated learning because it *marked* the preceding choice response in memory. Thomas, Lieberman, McIntosh, and Ronaldson (1983) showed that a "marker" presented immediately before the choice response improved learning as effectively as one presented afterwards. Similarly, it could be argued that handling the animals when they are placed

in the radial maze at the beginning of a session might "mark" the first arm choice of the study phase. This first choice would consequently be remembered better, leading to a primacy effect.

The rats in the present study were handled before the start of the study phase as well as after the fifth choice had been made, when the rats were placed into their home cages, and so if handling per se would lead to marking of choices, then at the longer delays one would expect better recall of the fifth as well as the first arm choice, which was not the case. It could be argued that handling *before* choice 1 is more similar to the situation during the test phase, when the animals are also handled *before* the choice is made. Handling would then provide a specific "retrieval cue" (Tulving & Osler; 1968, cf. Lieberman et al., 1979), leading to better recall of the first arm choice. The possible contribution of handling to the primacy effect might be tested by placing the rat into the apparatus some time before the start of a trial. It is difficult to account for the delay-dependent effects in terms of differential attention to the first item of the list.

Several different theories have been proposed to account for serial position effects in human memory. On the basis of their results, Wright et al. (1985) argue against single process theories in favour of "dual process interference theory". The aforementioned finding of the present study, that recall of the first item of the list is relatively stable at the different retention intervals, does not rule out an explanation of the results along the lines of the two-process theory of Atkinson and Shiffrin (1968). This would imply a short-term memory buffer for spatial working memory, underlying the recency effect. Primacy effects would then be a result of increasing transfer of items to long-term memory through a process like "rehearsal".

Maki (1986) has advocated the use of the concept of "intermediate-term memory" to explain the results of his experiments with electroconvulsive shock in the radial arm maze (cf. Maki, 1985; MacPhail, 1986; Bureš, Burešová, & Bolhuis, 1987). The results of previous experiments provide some support for the idea of an intermediate-term memory, involved in information processing in the radial maze. Several studies have shown that, although spatial working memory is relatively stable, it nevertheless decays exponentially, with a time course of a few hours, dependent upon the nature and the amount of previous training (Markowska, Burešová, & Bureš, 1983; Bolhuis, Burešová, & Bureš, 1985; Bolhuis et al., 1986; Strijkstra & Bolhuis, 1987). Long-term memory is usually thought to be important for a much longer period, for instance in the case of what Olton et al. (1979) have called "reference memory". More experiments using the present paradigm are needed to be able to test the predictions that can be made on the basis of different theories. In view of the similarities of the present findings with phenomena in human memory for lists of items, the paradigm used may be useful for the development of animal models of human memory failure.

## REFERENCES

Atkinson, R. C. & Shiffrin, R. M. (1968). Human memory: A proposed system and its control processes. In K. W. Spence & J. T. Spence (Eds.), *The psychology of learning and motivation: Advances in research and theory*, Vol. 1 (pp. 89–195). New York: Academic Press.

Baddeley, A. D. (1976). *The psychology of memory*. New York: Basic Books.

Bolhuis, J. J., Bijlsma, S., & Ansmink, P. (1986). Exponential decay of spatial memory of rats in a radial maze. *Behavioral and Neural Biology, 46*, 115–122.

Bolhuis, J. J., Burešová, O., & Bureš, J. (1985). Persistence of working memory of rats in an aversively motivated radial maze task. *Behavioural Brain Research, 15*, 43–49.

Bureš, J., Burešová, O., & Bolhuis, J. J. (1987). Processing temporally discontiguous information is neither an exclusive nor the only function of the hippocampus. *Behavioral and Brain Sciences, 10*, 154–155.

Craik, F. I. M. (1970). The fate of primary memory items in free recall. *Journal of Verbal Learning and Verbal Behavior, 9*, 143–148.

DiMattia, B. V., & Kesner, R. P. (1984). Serial position curves in rats: Automatic versus effortful information processing. *Journal of Experimental Psychology: Animal Behavior Processes, 10*, 557–563.

Gaffan, D. (1977). Recognition memory after short retention intervals in fornix-transected monkeys. *Quarterly Journal of Experimental Psychology, 29*, 577–588.

Gaffan, D. (1983). A comment on primacy effects in monkeys' memory for lists. *Animal Learning & Behavior, 11*, 144–145.

Gaffan, D. & Weiskrantz, L. (1980). Recency effects and lesion effects in delayed non-matching to randomly baited samples by monkeys. *Brain Research, 196*, 373–386.

Kesner, R. P., Measom, M. O., Forsman, S. L., & Holbrook, T. H. (1984). Serial position curves in rats: Order memory for episodic spatial events. *Animal Learning & Behavior, 12*, 378–382.

Kesner, R. P. & Novak, J. (1982). Serial position curve in rats: Role of the dorsal hippocampus. *Science, 218*, 173–174.

Lieberman, D. A., McIntosh, D. C., & Thomas, G. V. (1979). Learning when reward is delayed: A marking hypothesis. *Journal of Experimental Psychology: Animal Behavior Processes, 5*, 224–242.

MacPhail, E. M. (1980). Short-term visual recognition memory in pigeons. *Quarterly Journal of Experimental Psychology, 32*, 521–538.

MacPhail, E. M. (1982). *Brain and intelligence in vertebrates*. Oxford: Clarendon Press.

MacPhail, E. M. (1986). Animal memory: Past, present and future. *Quarterly Journal of Experimental Psychology, 38B*, 349–364.

Maki, W. S. (1985). Three-store theories of memory. *Behavioral and Brain Sciences, 8*, 505–506.

Maki, W. S. (1986). Distinguishing between new and used traces: Differential effects of electroconvulsive shock on memories for places presented and places passed. *Quarterly Journal of Experimental Psychology, 38B*, 397–423.

Markowska, A., Burešová, O., & Bureš, J. (1983). An attempt to account for controversial estimates of working memory persistence in the radial maze. *Behavioral and Neural Biology, 39*, 97–112.

Mazuryk, G. F. (1974). Positive recency in final free recall. *Journal of Experimental Psychology, 103*, 812–814.

Murdock, B. B., Jr. (1962). The serial position effect in free recall. *Journal of Experimental Psychology, 64*, 482–488.

Olton, D. S. (1985). The temporal context of spatial memory. *Phil. Trans. R. Soc. Lond., B 308*, 79–86.

Olton, D. S., Becker, J. T., & Handelmann, G. E. (1979). Hippocampus, space and memory. *Behavioral and Brain Sciences, 2*, 313–366.

Olton, D. S. & Samuelson, R. J. (1976). Remembrance of places passed: Spatial memory in rats. *Journal of Experimental Psychology: Animal Behavior Processes, 2*, 97–116.

Olton, D. S. & Schlosberg, P. (1978). Food searching strategies in young rats: Win–shift predominates over win–stay. *Journal of Comparative and Physiological Psychology, 92*, 609–618.

Olton, D. S. & Werz, M. A. (1978). Hippocampal function and behavior: Spatial discrimination and response inhibition. *Physiology & Behavior, 20*, 597–605.

Roberts, W. A., & Kraemer, P. J. (1981). Recognition memory for lists of visual stimuli in monkeys in humans. *Animal Learning & Behavior, 9*, 587–594.

Roberts, W. A. & Smythe, W. E. (1979). Memory for lists of spatial events in the rat. *Learning and Motivation, 10*, 313–336.

Rundus, D. (1971). Analysis of rehearsal processes in free recall. *Journal of Experimental Psychology, 89*, 63–77.

Sands, S. F. & Wright, A. A. (1980). Serial probe recognition by a rhesus monkey and a human with 10- and 20-item lists. *Journal of Experimental Psychology; Animal Behavior Processes, 6*, 386–396.

Strijkstra, A. M. & Bolhuis, J. J. (1987). Memory persistence of rats in a radial maze varies with training procedure. *Behavioral and Neural Biology, 47*, 158–166.

Suzuki, S., Augerinos, G., & Black, A. H. (1980). Stimulus control of spatial behavior on the eight-arm maze in rats. *Learning and Motivation, 11*, 1–18.

Thomas, G. V., Lieberman, D. A., McIntosh, D. C., & Ronaldson, P. (1983). The role of marking when reward is delayed. *Journal of Experimental Psychology: Animal Behavior Processes, 9*, 401–411.

Thompson, R. K. R. & Herman, L. M. (1977). Memory for lists of sounds by the bottle-nosed dolphin: Convergence of memory processes with humans? *Science, 195*, 501–503.

Tulving, E. & Osler, S. (1968). Effectiveness of retrieval cues in memory for words. *Journal of Experimental Psychology, 77*, 593–601.

Winer, B. J. (1971). *Statistical principles in experimental design* (2nd ed.). New York: McGraw-Hill.

Wright, A. A., Santiago, H. C., Sands, S. F., Kendrick, P. F., & Cook, R. G. (1985). Memory processing of serial lists by pigeons, monkeys, and people. *Science, 229*, 287–289.

*Manuscript received 14 September 1987*